

1961. Studi di un'entomologia sugli Imenotteri superiori. Boll. Ist. Entomol. Univ. Bologna 25: 1-659.
- Grothaus, R. H. 1962. The biology of the species of *Ceratina* in Indiana. Unpublished Master's thesis, Purdue Univ., Lafayette, Ind. 201 p.
- Horne, C. 1870. Notes on the habits of some hymenopterous insects from the northwest provinces of India. Trans. Zool. Soc. London 7(1872): 161-96.
- Howard, L. O. 1890. A North American *Arima* and its habits. Insect Life 2: 365-7.
1892. The habits of *Melittobea*. Proc. Entomol. Soc. Wash. 2: 244-8.
- Hurd, P. D., Jr. 1958. Observations on the nesting habits of some New World carpenter bees with remarks on their importance in the problem of species formation (Hymenoptera: Apoidea). Ann. Entomol. Soc. Amer. 51: 365-75.
- Hurd, P. D., Jr., and J. S. Moure. 1963. A classification of the large carpenter bees (Xylocopini) (Hymenoptera: Apoidea). Univ. Calif. Pub. Entomol. 29: 1-344.
- Krombein, K. V. 1960. Biological notes on some Hymenoptera that nest in smilax pith. Entomol. News 71: 29-30.
- MacSwain, J. W. 1945. Notes on the habits of the predator *Cynodontera oxyptera* Say with a description of the pupa (Coleoptera, Cleridae). Pan-Pacific Entomol. 21: 97-100.
- Malyshev, S. I. 1912. Die Ceratien und ihre Parasiten. Trav. Soc. Imper. Nat. St.-Petersbourg, C.R. Séances 43(1): 252-5, 276-7.
1965. Lebensweise und Instinkte der primitiven Schlupfwespen Gasterulidae (Hymenoptera). Zool. Jahrb. (Syst.) 92: 239-88.
- Michener, C. D. 1961. Probable parasitism among Australian bees of the genus *Allocladophora* (Hymenoptera, Apoidea, Ceratini). Ann. Entomol. Soc. Amer. 54: 532-4.
- Packard, A. S. 1869. Guide to the Study of Insects. Naturalists' Agency, Salem, Mass. 702 p.
- Parker, F. D., and R. M. Bohart. 1960. Host-parasite associations in some twig-nesting Hymenoptera from western North America. Pan-Pacific Entomol. 42: 91-98.
- Pérez, J. 1889. Les Abeilles. Librairie Hachette et Cie, Paris, 548 p.
- Rau, P. 1922. Ecological and behavior notes on Missouri insects. Trans. St. Louis Acad. Sci. 24: 1-71.
1928. The nesting habits of the little carpenter-bee, *Ceratina calcarata*. Ann. Entomol. Soc. Amer. 21: 380-97.
- Schmiedeknecht, O. 1930. Die Hymenoptera Nord- und Mitteleuropas. Gustav Fischer, Jena. 1062 p.
- Seyrig, A. 1926a. Études sur les Ichneumonides. Eus 2: 113-33.
- 1926b. Observations sur les Ichneumonides. Ann. Soc. Entomol. France 95: 157-72.
- Slobodchikoff, C. N. 1967. Biological observations on *Grocla californica* with a description of the larva and pupa. Pan-Pacific Entomol. 43: 161-8.
- Townes, H. S. Memoir, and M. Townes. 1965. A catalogue and reclassification of the eastern Palaearctic Ichneumonidae. Mem. Amer. Entomol. Inst. 5: 1-661.
- Viereck, H. L. 1904. A new cryptine from the nest of *Ceratina dupla*. Entomol. News 15: 333-5.
1910. Order Hymenoptera. In: J. B. Smith, Ann. Rep. New Jersey State Mus. (1909): 579-699.
1916. The Hymenoptera or wasp-like insects of Connecticut. Bull. Conn. Geol. Nat. Hist. Surv. 22: 1-824.
- Wallace, G. 1954. A new wasp of the genus *Habritis* (Pteromalidae: Hymenoptera) from Wisconsin and New York. Ann. Carnegie Mus. 33: 199-200.
- Washburn, F. L. 1918. The Hymenoptera of Minnesota. 7th Rep. State Entomol. Minn. p. 145-240.
- Waters, N. D. 1966. Parasites, predators and nest destroyers of the alfalfa leafcutter bee. Idaho Curr. Inform. Serv. no. 25, 3 p.
- Zabriskie, J. L. 1890. [Untitled note.] Entomol. Amer. 6: 100.

The Morphology and Histology of the Hymenopterous Poison Apparatus. III. *Eciton hamatum* (Formicidae)¹

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ABSTRACT

The poison apparatus of *Eciton hamatum* (F.) is described and illustrated. In this species, as in other Dorylinae and in 2 genera of Ponerinae, the furcula is lacking. The anterior extension of the sting bulb functions in the place of this major sclerite, which reportedly is present in all wasps and stinging ants. Two muscles (muscles deflecting and rotating muscles of the sting) which insert on the furcula of most aculeates, insert on this anterior extension to cause deflection of the sting and a pivoting

action. The significance of the association between these 2 muscles and the furcula or sting bulb may involve the ponerine-doryline relationship. The origin of the furcula and the morphology and histology of associated soft parts which make up the poison apparatus are discussed. The venom produced by *E. hamatum* is proteinaceous, and contains a hemolysin. The chemistry of the venoms produced by stinging ants is discussed.

The reaction of human beings to the sting of *Eciton hamatum* (F.) is comparatively mild (Rettemeyer 1963), although this species has well developed glandular and reservoir regions and a functional sting apparatus. Whelden (1963) described parts of the poison apparatus of this species and *E. burchelli* (Westwood). Most of that investigation was concerned with

soft parts and very little consideration was given to the sclerites. The present investigation was initiated as part of a comparative study of the hymenopterous poison apparatus, dealing particularly with the perennating sclerites. A more detailed account of previous investigations was presented by Hermann and Blum (1966).

MATERIALS AND METHODS

Workers of *E. hamatum* were collected at Limón, Cacha Nana Province Ecuador from September to

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December 1964. In some cases, live specimens were sectioned immediately after collection, to examine the vital parts. Other workers were fixed in alcoholic Bouin's fluid and later sectioned in the manner prescribed for *Paraponera clavata* (F.) (Hermann and Blum 1966). In addition, the poison apparatuses of major workers were cleared and mounted on slides for examination of the sclerites.

RESULTS

Poison Sac.—The poison sac (PS, Fig. 1, A and B) is usually rounded to oval when full, the shape depending on the amount of fluid within it. A full sac is usually distinctly marked off from the slender main duct (MD).

Regions of the poison sac and gland are essentially the same histologically as those mentioned for *P. clavata* (Hermann and Blum 1966). The sac consists of a crinkled, chitinous tunica propria which surrounds an invaginated layer of the same composition as the convoluted gland (CG). The sac is covered by simple squamous epithelium (SE), the nuclei and topoplasmic borders of which are often very difficult to see. This epithelial layer is surrounded by a layer of transverse striated muscle (CM). The invaginated portion of the sac is similar in cellular composition to the external region of the sac, i.e., it is composed of simple squamous epithelium. In fact, this invagination is merely a continuation of the external tunica propria.

The main duct from the poison sac to the sting bulb (SB) has more extensive crinkling than the sac itself. Here is some decrease in diameter of the main duct from its distal to its proximal region (Fig. 1, A). The cellular makeup of the main duct, identical to that of the poison sac, consists of a layer of simple squamous epithelium.

Free Filaments.—The free filaments leave the sac at its base (FF, Fig. 1, A and H). Whelden (1963) stated that these free filaments arise from the anterior end of the sac. However, we have examined numerous fresh sacs, and have never found this to be the case. A common duct extends from the surface of the sac and forks into the individual free filaments. Its condition is similar to that found in *Paraponera* (Hermann and Blum 1966) and *Myrmecia* (Cavillat, 1964). The distal ends of the free filaments are positioned anteriorly in the gaster. We found no definite pattern in their position within the gaster such as was mentioned by Whelden (1963), although the filaments always seemed to have some connections with structures at their distal ends. The filaments have a uniform diameter throughout their length, similar to the filaments of *Paraponera*.

The filaments are composed of simple cuboidal cells with a line an undulating lumen. The cells in the filaments possess large nuclei and granular cytoplasm.

Convoluted Gland.—This structure (CG, Fig. 1, A and B) is found within the poison sac. It consists of numerous polygonal cells and ducts which we believe are responsible for the synthesis of venom and its passage into the sac proper.

Dufour's Gland.—Dufour's gland (DG, Fig. 1, A) extends into the gaster to much less a degree than the poison sac. This gland is an elongate sac, the duct of which is not of a uniform appearance throughout its length. Dufour's gland is 1.0–1.3 mm long and 0.30–0.35 mm in diam. It is composed of simple columnar cells (CE, Fig. 1, E, F, and G), which are often quite elongated. The gland is encircled by a single layer of circular muscle (CM). The lumen is very irregular in places, especially in the portion of the gland that is within the sting bulb (Lu, Fig. 2, C). Distal in the gland the lumen is usually large, but as the gland enters the sting bulb the lumen often becomes obscure. Throughout most of the gland the nuclei of the columnar cells are centrally situated within the cell. Where Dufour's gland terminates in the anterior half of the sting bulb, the nuclei are found near the cell base (Fig. 2, C). Cells at that location are often low columnar.

As in the case in other ants, Dufour's gland enters the sting bulb just ventrad to the main duct of the poison sac (Fig. 2, C). A slender duct (DE) continues posteriorly from these columnar cells for a short distance before its lumen opens directly into the sting bulb. This duct is surrounded by an extensive supply of short muscles (Mu) which function as part of a mechanism, completely separate from the poison sac and main duct, to open and close Dufour's gland. A simple layer of cuboidal cells (Cu) can be seen around the base of Dufour's gland and surrounding the slender duct which empties into the sting bulb.

Skeletal Components of the Sting.—Whelden (1963) did not discuss the sclerites of the poison apparatus of this species, although he made some simple illustrations of the connections of the poison sac and Dufour's gland with the sting bulb. He also illustrated a transverse section of the sting bulb and lancets. However, the most significant differences between this species and species from other subfamilies seems to be involved with the skeletal components of the sting.

When the sting of *E. hamatum* workers is in a completely retracted position, it is usually hidden by the seventh abdominal plates. The gaster of workers of this species is elongate, the seventh tergal segment being quite reduced. The gaster is 3.0–3.5 mm in diam in the major worker.

The sting of major workers (St) is 1.6–1.8 mm long and 0.2 mm in diam at its largest point. The sting shaft (SS) is quite curved, especially on the distal half (Fig. 1, D and H). Sclerotization of this structure is quite extensive. A very significant feature associated with this structure is that the anterior and dorsal region of the sting bulb (SB) extends anteriorly (AE, Fig. 1, C and D; Fig. 2, A, D and E) for a considerable distance and actually receives muscles normally received by the furcula of other aculeate hymenopterans (muscles 3 and 4, Fig. 2, A).

The elongate, triangular plate (TP, Fig. 1, H; Fig. 2, A, B, and I; Fig. 3, B) reaches ventrad almost to the base of the entire sting when the lancets are in an almost completely retracted position. The rami of the

lancet (Ra 1) and oblong plate (Ra 2) show a broad curve from the latter structures to the sting bulb. There are no barbs on the distal end of the lancets (Fig. 3, B). Each lancet merely decreases in diameter to a sharp point. The valve (Va) is positioned on the anterior half of the lancet shaft, its height slightly greater than its width. The lancet measures 2.0–2.5 mm from the anterior bend just ventrad to the triangular plate to its distal tip, and 0.80–0.85

mm from the bend to the dorsum of the triangular plate (TP). The triangular plate has an anteroposterior length of 0.42 mm. The diameter of the lancet shaft varies from 0.02 to 0.03 mm. Each valve is 0.1 mm high and 0.1 mm wide.

The oblong plate (OP, Fig. 1, H; Fig. 2, A, B, and I) is not well sclerotized, the actual outline of the structure often being obscure. This plate lies mesad to the triangular plate (Fig. 2, I) and retains

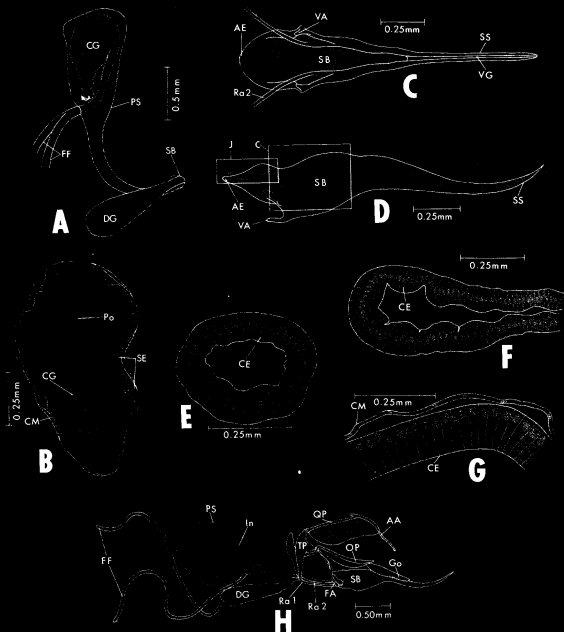


FIG. 1.—Soft parts and sclerites which compose the poison apparatus of *E. hamatum*. A, poison sac and Dufour's gland. B, transverse section through poison sac. C, ventral view of sting. D, lateral view of sting. E, transverse section of Dufour's gland. F, sagittal section of Dufour's gland. G, enlargement of transverse section of Dufour's gland. H, relationship between sclerites and soft parts of the poison apparatus. Boxes J and C are represented as sagittal sections in Fig. 2, J and C, respectively.

close association with the posterior region of the latter structure. The oblong plates terminate at their articulation with the gonostylar processes (Go, Fig. 1, H; Fig. 2, A). Each gonostylus is 4.5–5.0 mm long, and the length of the oblong plate is 1.0–1.5 mm. The latter structure is equipped with sensory spines (Se) in a region near its articulation with the triangular plate (Fig. 2, B).

The fulcral arms (FA, Fig. 1, H; Fig. 2, A) are very slender. Their length (height) is 0.4–0.5 mm, and their greatest width (anteroposteriorly) is 0.03–0.04 mm. These very well sclerotized structures act as points of pivot for the sting when it is being deflected.

The quadrate plate (QP, Fig. 1, H; Fig. 2, A) extends posterior and slightly dorsal from its articulation with the triangular plate. It is not well sclerotized and its borders are often difficult to see. It measures 0.30–0.35 mm long, and has a T-shaped distal end.

The eighth hemitergites (SP, Fig. 3, A and C) are inserted dorsally by a sclerotized bar, a structure representing a remnant of the previous connection between 2 sides of the tergum. This structure covers most of the remaining sclerites associated with the sting.

The Skeletomuscular Apparatus.—With the exception of muscle 12, the levator muscle of the sting, all the muscles associated with the sting sclerites are similar to the muscles of *P. clavata*. The sting is held in a retracted and horizontal position by this muscle, which originates on the posterior border of the second ramus (Ra 2) and inserts on the anterior end of the sting bulb (Fig. 2, A). Contraction elevates the distal end of the sting after it has been deflected by muscle 3 during the sting act. Snodgrass (1935, 1956) and Foerster (1912) have reported this muscle elsewhere. The remaining muscles function in a manner identical to *Paraponera* and were described by Hermann and Blum (1966). Only a brief outline and summary of their function need be presented here.

Muscle 1 (Fig. 2, A) originates on the dorsal apodeme of the oblong plate, inserts on the lateral apodeme of the posterior apodeme of the quadrate plate, and results in the retraction of the lancets upon contraction. Muscle 2 originates on much of the lateral face of the oblong plate, inserts on the mesal border of the quadrate plate, and results in protracting the lancets. Contraction of muscle 3, which originates on the mesal border of the oblong plate and inserts on the lateral surface of the anterior extension of the sting bulb, results in deflection of the sting. Muscle 4 originates on the mesal border of the oblong plate, but in a position immediately mesad to its insertion on the dorsal region of the anterior extension of the sting bulb. Contraction causes a lateral movement of the anterior extension of the bulb to pivot the sting from side to side (Fig. 3, F and G). Muscles 5 and 6 function in a manner similar to the 2 muscles present in other aculeate forms except that their insertion is on the furcula in those forms and

contraction results more in a clockwise and counterclockwise rotation rather than a simple pivot (Fig. 3, D and E).

Muscle 5 originates on the mesal ventral border of the fulcral arm and inserts on the ventral wall of the poison duct within the sting bulb. Contraction results in the opening of the duct to allow for the flow of venom. Muscle 6 is antagonistic to muscle 5. It passes over the dorsum of the poison duct from the mesal surface of one fulcral arm to the other. Contraction results in closing the duct.

Muscle 7 extends from the mesal border of one oblong plate to the other and contraction tends to align the various sclerites which were manipulated during the stinging act.

Muscle 8 originates on the mesal surface of the anterodorsal region of the seventh abdominal sternite and inserts on the anteroventral region of the spiracular plate (Fig. 3, C). Contraction results in the depression of the entire sting mechanism. Muscle 9 (antagonistic to muscle 8) originates on the mesal border of the anteroventral region of the seventh abdominal tergite, inserts on the anterodorsal region of the spiracular plate, and results in the elevation of the entire sting mechanism upon contraction (Fig. 3, C).

Muscle 10 originates on the posteroventral region of the mesal surface of the spiracular plate and inserts on the lateral region of the quadrate plate (Fig. 3, C). Contraction results in a slight posterior and dorsal movement of the entire sting mechanism. Muscle 12 acts as a levator to elevate the sting after deflection. Muscle 11 (antagonistic to muscle 10) originates on the mesal surface of the spiracular plate and inserts on the dorsal surface of the quadrate plate (Fig. 3, C). Contraction causes the entire sting mechanism to move slightly anterior and ventrad to a depressed position.

Effects of the Sting.—The reaction of human beings to the sting of *E. hamatum* has been reported to be milder than to those of some other species in this genus (Rettenmeyer 1963), but Rettenmeyer (personal communication) also suggests that the sting of this ant is more effective than the stings of *E. d. dulcius* Forel, *E. d. crassinode* Borgmeier, *E. mexicanum* Roger, and *E. vagans* (Olivier). *E. hamatum* is one of the more specialized species of the Ectonini, and thus, less typical of that tribe. However, the sting of most species of the genus *Ecton* is not considered to be very painful to human beings.

E. hamatum seems to be less efficient in capturing prey than some other species of the Ectonini. However, efficiency in capturing prey is undoubtedly dependent upon the mode of attack and other behavioral factors, as well as on the potency of the venom and size of the sting.

Members of the genus *Ecton* probably prey on ants more than on any other group of arthropods. This preference was reported for *E. burchelli* by Rettenmeyer (1963). Workers have been seen entering and attacking ants in subterranean nests. Rettenmeyer stated that although many species of nondoryline ants

are captured by *E. hamatum*, he has not seen it prey on the ponerine *P. clavata*. However, *Paraponera* is preyed upon by *E. burchelli*.

Wasps, Orthoptera, and spiders are probably next in abundance among the booty taken by members of the genus *Eciton*. Rettenmeyer (1963) stated that the wasps attacked by *E. hamatum* are primarily the social Polybiinae and Polistinae (Vespidae). However,

whereas adult polybiine wasps are killed if they remain on the nest, such is seldom the fate of adult vespids, which abandon their nests to the attacking dorylines.

A large proportion of the potential prey always seems to escape. Even when the ants attack nests of social insects and the brood are completely killed, most of the adults escape. This may be due to a virtually

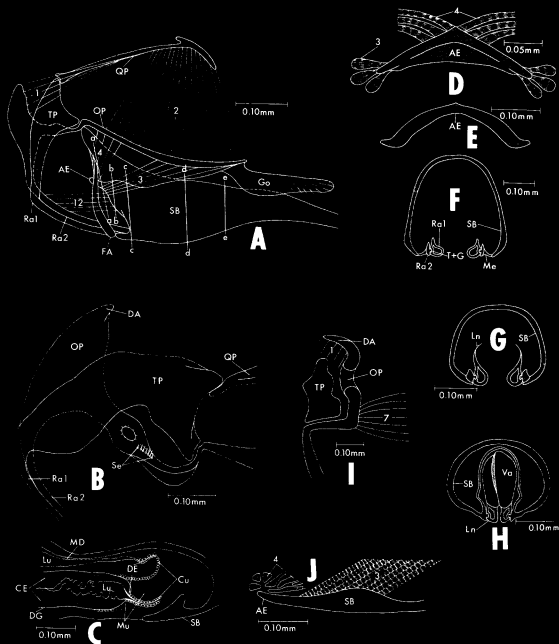


FIG. 2.—Sclerites and some muscular attachments in the poison apparatus of *E. hamatum*. A, lateral view of poison apparatus. B, enlargement of triangular and oblong plates. C, sagittal section through sting bulb as represented in box C of Fig. 1. D, D—H, transverse sections through sting at a-a, b-b, c-c, d-d, and e-e of A, respectively. I, dorsal view of triangular and oblong plates. J, sagittal section through anterior extension of sting bulb as represented in box J of Fig. 1. D.

ineffective sting or to a combination of factors, including those of an ethological nature. Since workers of *E. hamatum* often have difficulty in successfully stinging human beings (true chiefly of the smaller workers), it is not unlikely that they will find it difficult to penetrate the tough, sclerotized exoskeleton of many species of insects.

The venom of *E. hamatum* consists of a clear liquid which appears to be completely soluble in water. When exposed to air, the venom is rapidly converted to an amorphous solid which can be dissolved readily in water. When tested with pH paper, venom which issues from an everted sting produces an alkaline reaction; aqueous solutions of the venom are also strongly alkaline (pH = 9-10).

Probably the venom which issues from the extruded sting is primarily a product of the poison gland. When *E. hamatum* workers were allowed to sting either of us for a sustained period, subsequent dissection of the poison apparatus always revealed that the poison sac was collapsed. On the other hand, Dufour's gland was always turgid with its chartreuse secretion. At best, only a trace of the secretion from Dufour's gland can be present in the venom which is ejected at the sting site and as a consequence, the reaction resulting from an *Eciton* sting can be attributed almost exclusively to the natural products synthesized by the poison gland. It is also quite apparent that *E. hamatum*, like other stinging hymenopterans which we have examined, can rapidly secrete nearly the entire contents of its poison sac into the sting bulb while at the same time closing off the exit from Dufour's gland.

The venom which is collected as it issues from the extruded sting is rich in proteins but does not contain any detectable free amino acids. Venom samples which were analyzed by 2-dimensional paper chromatography (*n*-butanol:acetic acid:water, 4:1:1 and 2% aqueous pyridine) were characterized by the presence of strongly ninhydrin-positive material only at the origin. Hydrolysis of the venom (HCl:formic acid, 1:1) produced a large series of free amino acids, the most concentrated of which were glutamic acid, lysine, and leucine. Examination of the venom by gel electrophoresis revealed the presence of 4 proteins.

Like the poison gland products, the secretion from Dufour's gland is water insoluble. The chartreuse-colored liquid found in the reservoir of Dufour's gland is lighter than water and readily forms droplets on the surface when the gland is exposed in an aqueous medium. This secretion is Ninhydrin-negative and thus strongly contrasts to the proteinaceous constituents which are produced in the sting-associated gland, the poison gland.

The venom of *E. hamatum* was demonstrated to contain a hemolytic factor. Hemolysis was examined by capturing 3 poison sacs dissected from major workers in 0.1 ml of phosphate buffer (pH = 7.4), which was added 0.8 ml of a 2% suspension of rat red blood cells. Complete hemolysis occurred in 15 min.

DISCUSSION

E. hamatum is probably typical of the dorylines in producing a proteinaceous venom. We have examined also the venoms of species in the doryline genera *Neivamyrmex* and *Labidus*, as well as other species in the genus *Eciton*, and in all cases, proteins were present. Indeed, with the exception of the myrmecines *Solenopsis saccharissima* (F. Smith), *S. xyloni* McCook, and *S. geminata* (F.), no venom produced by stinging hymenopterans has been found to be protein-free. Hemolysins also have been found in the venoms of members of all the other subfamilies of ants which inject venom with a sting, and it is very probable that compounds capable of lysing red blood cells will be found commonly in ant venoms, as they are in the venoms of vertebrates.

E. hamatum is similar to ponerines, pseudomyrmecines, and myrmecines that we have examined in that the venom which is discharged through the sting originates mainly, if not completely, in the poison gland. Dufour's gland is always turgid after the venom issues from the sting and the nonprotein products of this gland clearly are not major constituents of the injected venom. It would be appropriate to ask: what is the function of the Dufour's gland secretion in the Formicidae? Although the secretion from this gland functions as a releaser of social behavior in the myrmecine genera *Pheidole* and *Solenopsis* (Wilson 1963), no function can be attributed to the products of this gland in any of the other formicid genera. In some genera—e.g., *Paraponera* (Hermann and Blum 1966)—Dufour's gland is larger than the poison sac and the reservoir of the former contains a large volume of secretion. The extensive development of this gland in many ant genera would serve to indicate that its secretion plays an important role in formicid biology. For ants as well as many other hymenopterous groups, the determination of the role of the Dufour's gland secretion represents a major unsolved problem.

The sclerites, muscles, and other associated parts of the poison apparatus of *E. hamatum* are essentially the same as those found in other aculeate hymenopterans. Some specific differences between the poison apparatus of *E. hamatum* and those of most Aculeatae are: (1) the position of departure by the free filaments from the poison sac, (2) the lack of barbs on the distal end of each lancet, and (3) the absence of a furcula which articulates with the anterior end of the sting bulb in other aculeates.

The free filaments extend from the base of the poison sac in this species, a condition which also occurs in the Myrmecinae, Ponerinae, Pseudomyrmecinae, and Formicinae. The free filaments extend from a position near the apex of the sac in myrmecines and dolichoderines. The slender appearance of the filaments in *E. hamatum* is also a condition found in the Myrmecinae, Ponerinae, Pseudomyrmecinae, and Formicinae, whereas in the Myrmecinae, the filaments have a larger diameter/length ratio. In the Dolichoderinae, the free filaments are oval.

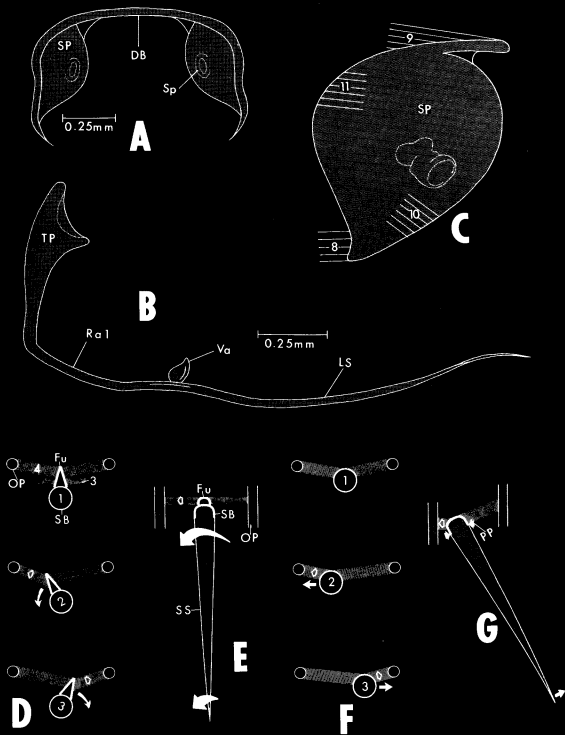


FIG. 3.—Some sclerites in the poison apparatus of *E. hamatum* and diagrammatic sketches illustrating the functional difference between the furcula and the anterior extension of the sting bulb. A, dorsal view of the spiracular plates. B, lateral view of the sting bulb. C, lateral view of the spiracular plate. D and E, illustration of a transverse section through the anterior region of the sting and a dorsal view of the sting of a furculate hymenopteran respectively, showing how muscle 4 rotates the sting. F and G, dorylinelike sting, illustrating the pivoting of the sting upon contraction of muscle 4.

The lack of barbs on the lancets of *E. hamatum* does not have any obvious significance, since there is no constant pattern among any members in the Formicidae. Thus, barbs are present on the lancets of many myrmecines, although they are absent in *Myrmica* (unpublished data). They are present in some pseudomyrmecines but have been reported to be absent in *Pseudomyrmex pallidus* (F. Smith) (Blum and Callahan 1963). They are generally present in the Ponerinae but are lacking in all the doryline species which we have examined.

The lack of a furcula in this and other species of the Dorylinae does have some interesting implications which may be very important in establishing the phylogenetic relationship of the army ants within the Formicidae.

The origin of the hymenopterous furcula has not been previously suggested. Other than for members of the Dorylinae and 2 species of the Ponerinae, all the stinging Hymenoptera that we have examined possess this sclerite. None of the New World dorylines (including members of the genera *Eciton*, *Labidus*, *Neivamyrmex*, *Nomamyrmex*, and *Cheliomyrmex*) as well as the Old World genera *Dorylus* (including subgenera *Dorylus*, *Typhlopone*, and *Anomma*) and *Aenictus*, possess a furcula. There is an anteriorly extended portion of the sting bulb in all New World dorylines examined, and anterolateral extensions in the Old World dorylines. The presence of muscles 3 and 4 in these doryline species and their insertion on the anterior and anterolateral extensions of the sting bulb indicates that the furcula and anterior region of the sting bulb are homologous structures. Since these structures are homologous, it seems evident that either the furcula has arisen from the anterior region of the sting bulb or fusion between the furcula and anterior region has taken place, to produce the condition found in the dorylines and some ponerines today.

The view that the furcula may have arisen from the sting bulb must be reconciled with several important considerations. First, it has been suggested that the dorylines may have arisen from poneroid stock (Brown 1954). Structural modifications of *Onychomyrmex* larvae and the wing venation in *Typhlopone* are suggestive of doryline characters. Also, it has been pointed out that several ponerine species illustrate doryline behavior such as group raiding and nomadism (Wilson 1958). If the dorylines have arisen from poneroid stock, the presence of a furcula would be the primitive condition, and fusion of the furcula to the sting bulb must have been the subsequent evolutionary step.

Secondly, the separation of a furcula from the sting bulb (sclerite elaboration) does not follow the rule of evolutionary reduction (Brown 1965). This rule states that "evolutionary change in a given character is more likely to be a reduction rather than an elaboration." Thus, fusion of the furcula to the sting bulb would support the rule, whereas the elaboration

arisen from poneroid stock, although based on behavioral and morphological considerations, dorylines and some ponerines share several common characters. In the past few years, more information on the dorylinelike ponerines has been accumulated than formerly, and Brown (personal communication) feels that there can be no reasonable doubt that *Onychomyrmex*, *Simopelta*, and the mass-foraging species-group of *Leptogenys* originated separately from all or any of the ponerine tribes. *Simopelta* and *Onychomyrmex* seem to have most army ant attributes, both behaviorally and morphologically. After careful examination of the sting sclerites in *O. hedleyi* Emery, *S. oculata* Gotwald and Brown, and *Sphinctomyrmex steinhillei* Forel, we have obtained the following interesting results: *Onychomyrmex* has a well-developed furcula. *Simopelta* possesses a dorylinelike sting lacking a furcula and has an anterior extension of the sting bulb that is the point of insertion of muscles 3 and 4. *Sphinctomyrmex* does not possess an anterior extension of the sting bulb, but muscles 3 and 4 are nevertheless inserted on the anteriormost region of the sting bulb.

A consideration of all these data leads us to the belief that the ponerine-doryline similarities may indicate a phylogenetic relationship between the 2 groups. However, the possession of a furcula by *Onychomyrmex* seems to indicate that similarities between it and the Dorylinae may represent nothing more than the convergence of characters.

Because many characters support the rule of evolutionary reduction, especially meristic characters, it is by no means impossible to find exceptions to the rule. In support of the hypothesis that the anterior bulb extension and furcula are homologous structures is the presence of the pair of muscles (3 and 4) which insert on these structures. In aculeate Hymenoptera, other than the Dorylinae and some of the dorylinelike ponerines, muscle 4 tends to rotate the sting. In the Dorylinae, contraction of muscle 4 tends to pivot the sting rather than rotate it. It is decidedly advantageous for an ant to be able to rotate its sting, since rotation permits the sting to be thrust in numerous directions. A pivoting sting, such as is found in all the doryline species examined, is much more limited in the direction of its thrusts. Because of the obvious importance of the sting in the biology of ants, it would operate as a selective disadvantage to lose a structure (the furcula) which contributes so markedly to the efficiency of action of the sting. This consideration would tend to support the hypothesis that the anterior bulb extension may have given rise to the furcula.

In a predatory group of ants such as the dorylines, the lack of an effective stinging mechanism would prove to be a very strong liability unless the ants have selected for the development of another highly efficient method of immobilizing prey. This problem appears to have been admirably solved by the Dorylinae through the use of the sting bulb.

the Old World dorylines, which have lost completely the ability to sting, are considered to bite with a severity which is never encountered in the New World dorylines, all of which can sting.

If the furcula has arisen from the anterior bulb extension, it would seem that 1 of 2 conditions prevailed in the early history of these ant species: (1) ants arose from wasps as 2 independent stocks (i.e., in a prefurcate, or dorylinelike, form and a furcate form). Although the prefurcate condition has not been reported in modern wasps, further investigations of wasp stings may reveal prefurcate species. (2) Ants arose from a prefurcate-type ancestor and the furcula has evolved independently in wasps and ants. All wasp species previously investigated possess this sclerite (including the Tiphidae).

That the ants are diphylectic has little support other than the possibility suggested by the prefurcate-furcate evidence presented in this paper. At present, neither morphological nor behavioral data provide any compelling evidence which indicates that the Formicidae are diphylectic. The possibility that the furcula evolved independently in ants and wasps seems to have some support. Selection pressure for the development of a furcula may have been, and still may be, great in those ants and wasps in which stinging plays an important ethological role. In the mutillid wasps, for example, we have found that selection has played an important role in the evolution of the furcula, so this sclerite has become extremely modified in both shape and function. Therefore, if the furcula did arise independently in the 2 groups, it seems as though the dorylines and a few ponerines may have retained the single primitive prefurcate form.

In conclusion, we feel that the furcula may be an important tool in understanding the phylogenetic sequence through which aculeate hymenopterans have evolved. Based on whether a prefurcate or a furcate condition is present, as well as on other morphological and behavioral evidence, it seems likely that the ponerine-doryline relationship may be close in some cases. We feel that much more morphological evidence is needed to support any hypothesis as to whether the anterior bulb extension is a pre- or postfurcate structure.

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ABBREVIATIONS USED IN FIGURES

AA	Anal arc
AE	Anterior extension of sting bulb
CE	Columnar epithelium
CG	Convolute gland
CM	Circular muscle
Cu	Cuboidal epithelium
DA	Dorsal apodeme of oblong plate
DB	Dorsal bar of spiracular plates
DE	Duct exit
DG	Dufour's gland
FA	Fulcral arms
FF	Free filaments
Fu	Furcula
Go	Gonostylus
In	Intima
Ln	Lancet
Lu	Lumen
MD	Main duct of poison sac
Me	Membrane
Mu	Muscle
OP	Oblong plate
Po	Poison
PP	Pivot point of sting
PS	Poison sac
QP	Quadrate plate
Ra 1	Ramus of first valvifer
Ra 2	Ramus of second valvifer
SB	Sting bulb
Se	Sensory setae
SE	Squamous epithelium
Sp	Spiracle
SP	Spiracular plate
SS	Sting shaft
T + G	Tongue and groove articulation
TP	Triangular plate
Va	Valve
VG	Ventral groove
VA	Ventral apodeme of sting bulb

Muscles:

- 1 Retractor of lancet
- 2 Protractor of lancet
- 3 Deflector of sting
- 4 Rotator or pivot of sting
- 5 Dilator of poison canal
- 6 Sphincter of poison canal
- 7 Aligner of lancets
- 8 First depressor of spiracular plate
- 9 First elevator of spiracular plate
- 10 Second depressor of spiracular plate
- 11 Second elevator of spiracular plate
- 12 Levator of sting

REFERENCES CITED

- Blum, M. S., and P. S. Callahan. 1963. The venom and poison glands of *Pseudomyrmex pallidus* (F. Smith). *Psyche* 70: 69-74.
- Brown, W. L. 1954. Remarks on the internal phylogeny and subfamily classification of the family Formicidae. *Insectes Sociaux* 1: 22-31.
1965. Numerical taxonomy, convergence, and evolutionary reductions. *Syst. Zool.* 14: 101-9.
- Cavill, G. W. K., P. L. Robertson, and F. B. Whitfield. 1964. Venom and venom apparatus of the bull ant, *Myrmecia gulosa* (Fabr.). *Science* 146: 79-80.
- Foerster, E. 1912. Vergleichend-anatomische Untersuchungen über den Stechapparat der Ameisen. *Zool. Jahrb. (Anat. Ontog.)* 34: 347-80.
- Hermann, H. R., Jr., and M. S. Blum. 1966. The morphology and histology of the hymenopterous poison apparatus. I. *Paraponera clavata* (Formicidae). *Ann. Entomol. Soc. Amer.* 59: 397-409.

- Rettenmeyer, C. W. 1963. Behavioral studies of army ants. Kansas Univ. Sci. Bull. 44: 281-465.
- Saunders, R. E. 1935. Principles of Insect Morphology. McGraw-Hill Book Co., Inc., New York. 667 p.
1956. Anatomy of the Honey Bee. Comstock Publishing Associates, Ithaca, N.Y. 334 p.
- Whelden, R. M. 1963. The anatomy of the adult queen and workers of the army ants *Eciton burchelli* Westwood and *Eciton hamatum* Fabricius. II. J. N.Y. Entomol. Soc. 71: 158-78.
- Wilson, E. O. 1958. The beginnings of nomadic and group-predatory behavior in the ponerine ants. Evolution 12: 24-31.
1963. The social biology of ants. Annu. Rev. Entomol. 8: 345-68.

Life History of the Incense-Cedar Wood Wasp, *Syntexis libocedrii* (Hymenoptera: Syntexidae)¹

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ABSTRACT

This heretofore rare wood borer heavily infested sapwood-sized incense-cedars on a forest burn near Viola, Calif., in 1963.

The life history was studied in the field and laboratory. The insect took 2 years to complete its development on the Viola burn. However, in other cases development can be completed in 1-3 years. Eggs are deposited in the sapwood; larvae can bore to a depth of 76 mm, and pupation

takes place at the end of the larval gallery near the surface of the sapwood. Adults emerge from the wood and make attacks on trees freshly fire-killed in July and August.

The insect's capacity to produce large populations and attack merchantable timber indicates that it should be considered a potential economic threat in fire-killed cedar.

Following several midsummer forest fires in Shasta and Modoc Counties in northern California, many specimens of the heretofore rare incense-cedar wood wasp, *Syntexis libocedrii* Rohwer, were collected. On a burned area near Viola, Shasta County, the first known males of the species were trapped (Wickman 1964a). Middlekauff (1964) described the males and summarized the known information on this insect. A large population of *S. libocedrii* developed on the Viola burn, providing enough insects to obtain data on life history and behavior.

MATERIALS AND METHODS

S. libocedrii was studied under natural field conditions and in the laboratory. Observations on host preference, gallery construction, emergence, and natural enemies were made on the Viola burn of August 1963. One year later, burned trees infested with larvae were felled. Log sections were brought to the Mt. Creek Forest Insect Laboratory,² where some logs were radiographed, some were split to obtain larvae, and others were placed in rearing cages. Only ♀ *S. libocedrii* emerged in 1964, but larvae were still plentiful in the logs. The study was continued through the summer of 1965 by using periodic radiography (Fig. 1) and log splitting to follow insect development. Moisture content of the logs was measured by weighing oven-dried samples.

In August 1965, mated and unmated newly emerged males were caged with fresh cedar logs—both scorched and unscorched in each cage—to observe disposition, to check on female parthenogenesis, and

to study the development of the attacks. Logs were scorched by burning with a blowtorch the bark of freshly felled trees.

DISTRIBUTION, HOST, AND DAMAGE

S. libocedrii has been collected only in the central Sierra Nevada and the Cascade and Siskiyou Mountains of northern California, and only from a single host—incense-cedar, *Libocedrus decurrens* Torr. Conceivably, the insect could occur throughout the range of its host, from southern Oregon southward through California and western Nevada to Lower California. Before recent collections, only 3 specimens had been recorded. Therefore, any conclusions on insect distribution are tentative.

Damage consists of insects boring several inches into the sapwood of incense-cedar. Before the Viola burn, the insect was never numerous enough to be considered a wood-destroying pest. However, at Viola, attacks were heavy enough on some cedars to have degraded salvaged lumber.

DESCRIPTION, LIFE HISTORY, AND BEHAVIOR

Adults.—*Syntexis* was first described by Rohwer (1915) from the female (Fig. 2). Insects reared in logs from the burn for the study reported in this paper consisted of 68 ♀ ranging from 8 to 16 mm long, averaging 13 mm; and 11 ♂ specimens (10 trapped on the burn) ranging from 8 to 12 mm long, averaging 11 mm. Adults reared from laboratory matings consisted of 17 ♀ ranging from 6 to 11 mm long, averaging 8 mm; and 3 ♂ ranging from 6 to 8 mm long, averaging 7 mm (Fig. 3). The smaller size might be due to the lower moisture content of the caged logs or to some other laboratory artifact.

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² Maintained by the Pacific Southwest Forest and Range Experiment Station in Shasta County, Calif.